Reproductive biology, age structure, and diet of *Mastomys natalensis* (Muridae: Rodentia) in a Swaziland grassland

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Abstract

The time of reproduction, monthly changes in age structure and diet of *Mastomys natalensis* were investigated in a subtropical grassland in Swaziland. Mice were collected monthly over a 25 month period. The ages of *Mastomys natalensis* individuals were estimated using eye lens weight. Pregnant females and scrotal males were recorded in the wet season only, with interannual differences in the initiation of breeding being correlated with rainfall. Monthly changes in age structure of *M. natalensis* are determined by the entry of young during the wet season and the death of adults, that were previously reproductive, in the dry season. The stomach contents of *M. natalensis* consisted predominantly of vegetative plant matter in the dry season, with seeds and arthropods having contributed significantly in the wet season.

Key words: Mastomys natalensis, reproduction, diet, age-structure

Introduction

The multimammate mouse *Mastomys natalensis* (A. Smith, 1834) is a widespread African murid rodent of great economic importance (de Graaf 1981; Skinner and Smithers 1990). The reproductive biology and population structure of *M. natalensis* has been intensively investigated at only one study site in Tanzania (Telford 1989; Leirs and Verheyen 1995). In contrast, existing knowledge of this species in southern Africa is based on several scattered, short-term studies (Coetzee 1965; Chidumayo 1984; Bronner et al. 1988). Furthermore, the age of mice captured for these southern African studies were estimated using toothwear, a technique which is known to be inaccurate (Morris 1972).

The objectives of this study were to investigate the time of reproduction, monthly population age-structure and seasonal changes in diet of *M. natalensis* in a subtropical grassland in the Middleveld of Swaziland.

Material and methods

The study area was situated at eKundizeni Farm (26°33′S; 31°16′E) near Matsapha, Swaziland, approximately 1 km away from the site described in Monadlem and Perrin (1996). This region receives most of its rainfall between October and March, but the onset of rains differs between years. The mean annual rainfall recorded over 30 years by the University of Swaziland Meteorological Station, located 8 km to the east of the study site (at a similar altitude of 650–700 m a.s.l.), is 928 mm. Mean minimum temperature for July 1995 was 7.6 °C, while mean maximum temperature for February 1996 was 27.3 °C. During the study period, rainfall was recorded monthly at eKundizeni Farm.

Small mammals were trapped monthly using Sherman live-traps and commercial back-break kill-traps set in lines. The population dynamics of *Mastomys natalensis*, studied at a site approximately 2 km away, has been reported elsewhere (Monadjem and Perrin 1998). These lines were rotated on a monthly basis to avoid trapping the same line two months consecutively. Sherman traps were set on one or two nights per month from October 1995 to March 1997, whereas kill-traps were set from October 1995 to October 1997. Traps were set five metres apart and were not pre-baited. The mice captured with Sherman traps were returned to the laboratory where they were killed with chloroform, measured and their reproductive condition assessed. Reproductive condition was assessed following Leirs and Verheyen (1995). In males, the position and length of the testes, the size of the seminal vesicles and epididymal tubuli was recorded. In the females, the condition of the uterus (filiform, normal, oestrous or pregnant), the number of embryos and placental scars was recorded.

The eyes of *Mastomys natalensis* were removed immediately after death and the eye lenses were prepared for weighing following Perrin (1979). The eyes were fixed in 10% formalin. After fixation, the lenses were removed and oven dried for 7 days at 80 °C. Each lens was weighed separately on an electronic balance. The age of each mouse was estimated using the regression line of lens weight on age in days in Leirs and Verheyen (1995):

 $w = -10.46088 + 4.35076 \times \ln(a)$

where: w = dry eye lens weight in mg; and a = age in days. Mice were assigned to one of seven age classes (<99 days, 100-159 days, 160-219 days, 220-279 days, 280-339 days, >340 days). Mastomys natalensis reaches first oestrous at a mean age of 104 days (Johnston and Oliff 1954) and, hence, the first age class includes mostly immature individuals. The remaining age classes were arbitrarily set at 60 day intervals.

Mice captured in the kill-traps were returned to the laboratory where their reproductive condition and stomach contents were assessed. Commencing in November 1996, the stomachs of the kill-trapped mice were removed for stomach content analysis following Kerley (1989) and Monadjem (1997). Four dietary categories were recognized: foliage (vegetative plant material), seeds, arthropods, and unidentified material. The importance of each food type was expressed both as a frequency of occurrence and a proportional (percentage) contribution. Frequency of occurrence was calculated as the number of stomachs in which a particular food type was observed. Percentage contribution was determined by examining the stomach contents through a dissection microscope. The relative contribution of each food type in the microscope field was estimated for five randomly placed fields.

Results

Total monthly rainfall during the study period is shown in figure 1. The total rainfall for the period October 1995 to September 1996 was 1368 mm, and for the period October 1996 to September 1997 was 1101 mm. Rainfall during the study period was above the long-term mean (928 mm) for the area.

The number of *Mastomys natalensis* captured in each month is shown in table 1. Other species of small mammal captured were: *Crocidura mariquensis* Roberts, *Crocidura hirta* Peters, *Rhabdomys pumilio* (Sparrman), *Mus minutoides* A. Smith, *Dendromus mystacalis* Heuglin, *Otomys angoniensis* Thomas, *Lemniscomys rosalia* (Thomas), and *Steatomys pratensis* Peters.

Reproduction

M. natalensis was not reproductively active throughout the study period (Fig. 2). Males were scrotal in 14 months of the study and females were pregnant during 8 months. Reproductive activity was correlated with rainfall in both males ($r_{23} = 0.802$, P < 0.001) and females ($r_{23} = 0.569$, P < 0.01). Reproductive activity in females was also correlated with rainfall one and two months previously ($r_{22} = 0.622$, P < 0.01; $r_{21} = 0.668$, P < 0.001, respectively), while in males it was only correlated with rainfall one month previously ($r_{22} = 0.589$, P < 0.01). There was very little sign of reproductive activity, in either sex, during the dry season between April and October.

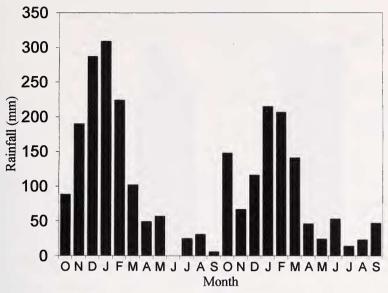
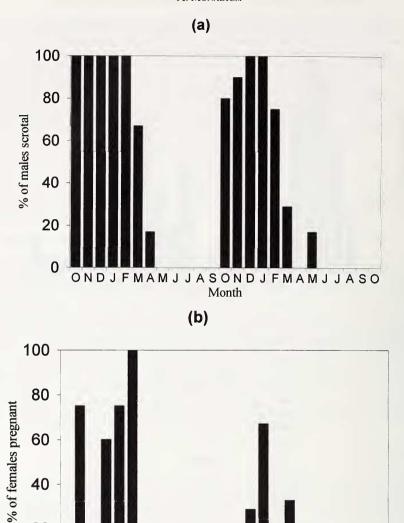


Fig. 1. Total monthly rainfall at eKundizeni Farm, Swaziland from October 1995 to October 1997.

Table 1. Number of trap-nights and number of captures of Mastomys natalensis.

Date	Numbers			
	Trap-nights	M. natalensis		
1995				
October	75	6		
November	45	10		
December	120	5		
1996				
January	80	16		
February	60	5		
March	120	5		
April	60	11		
May	60	9		
June	No trapping			
July	60	10		
August	60	8		
September	300	14		
October	150	13		
November	150	15		
December	150	29		
1997				
January	150	5		
February	150	10		
March	150	8		
April	40	7		
May	40	8		
June	40	8		
July	40	5		
August	40	4		
September	40	4		
October	40	2		



20 0 ONDJFMAMJJASONDJFMAMJJASO Month Fig. 2. The proportions (%) of Mastomys natalensis: (a) males with scrotal testes, and (b) pregnant fe-

males, trapped between October 1995 and October 1997.

The initiation and intensity of breeding in M. natalensis varied between the two years. In the 1995/6 breeding season, all males were fully scrotal at the beginning of the study in October. In the 1996/7 breeding season, however, only 80% of the males were scrotal in October. This interannual difference was even more pronounced in females, where 75% of females were pregnant in November 1995 while none were pregnant in November 1996 (and only 33% were pregnant in December 1996). Thus, M. natalensis initiated breeding approximately one month later in the 1996/7 breeding season than in the previous season.

Table 2. Mean mass and litter size (\pm SE) of female *Mastomys natalensis* of different age classes. Row values with different superscripts indicate a significant difference (ANOVA, P<0.05) among age classes.

	Age class			
	<6 months	6 to 8 months	>8 months	
Sample size	22	17	21	
Mean mass	30.2 ± 2.6^{a}	30.2 ± 1.8^{a}	38.6 ± 1.8^{b}	
Mean litter size	13.8 ± 2.1^{a}	10.7 ± 1.5^{a}	9.9 ± 1.6^{a}	

The litter size of M. natalensis was 11.4 (n = 17; range: 3–24). There were no significant differences in the litter size of M. natalensis between females of ages less than six months, 6 to 8 months, and greater than 8 months (ANOVA, P > 0.05; Tab. 2). Females older than 8 months, however, weighed more than females in the two younger categories.

The ages of 146 *M. natalensis* (60 females and 86 males) were estimated using eye lens weight. It was thus possible to estimate the dates of birth for these individuals. Most mice were born between November and March (Fig. 3), with only a single individual being born between July and September in 1995 and none between July and November in 1996.

There was a significant, albeit weak, correlation between age and body mass in male M. natalensis ($r_{86} = 0.453$, P < 0.001).

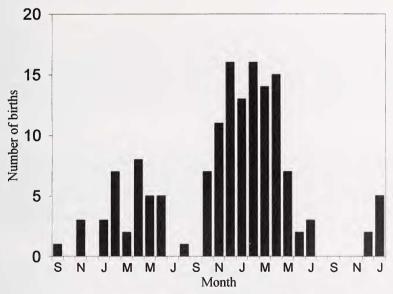


Fig. 3. Numbers of *Mastomys natalensis* born per month (based on age estimated from eye lens weight) between September 1994 and January 1997.

Age structure

The monthly age structure of *M. natalensis*, based on the mice that were aged by the eye lens weight technique, is shown in table 3. Immature mice (first age class) entered the population in December in the 1995/6 season, but only in February in the 1996/7 season. This corresponds to the delay in reproductive activity recorded in the 1996/7 season. Immature mice were recorded between December 1995 and July 1996 with a peak in April,

Table 3. Seasonal changes in age class structure of *Mastomys natalensis* between October 1995 and March 1997 at eKundizeni Farm, Swaziland. Numbers are the percentages of individuals recorded in each age class.

	·		Age class (in days)					
Month		n	<99	100–159	160–219	220–279	280–339	>340
1995	Oct	6	_	50	17	17	17	_
	Nov	9	_	-	33	22	44	-
	Dec	4	25	-	25	25	_	25
1996	Jan	15	20	7	7	40	13	13
	Feb	4	25	25	_	25	_	25
	Mar	4	50	25	_	_	_	25
	Apr	11	73	27	_	_	_	_
	May	9	22	78	_	_	_	_
	Jun	No data						
	Jul	10	20	40	10	20	_	10
	Aug	8	_	13	25	38	25	_
	Sep	3	_	_	33	33	33	_
	Oct	13	_	_	31	46	8	15
	Nov	14	_	29	43	7	7	14
	Dec	24	_	_	4	67	17	13
1997	Jan	2	_	_	_	100	_	_
	Feb	6	83	_	_	_	17	_
	Mar	3	67	-	-	33	-	-

but were absent between August 1995 and January 1996. Very few mice were estimated to be older than twelve months (the oldest mouse being aged at 480 days). Individuals in the last age class were captured in the wet season and the late dry season, but were absent in the late wet season and early dry season (between April and September).

Diet

The stomach contents of *Mastomys natalensis* (n = 57) consisted predominantly of foliage, with seeds and arthropods present at lower frequencies. Seasonal changes in the diet of *M. natalensis* are shown in figure 4. In the dry season (between June and October), the diet of *Mastomys natalensis* consisted entirely of foliage. Seeds were an important component of the diet in the wet months between November and May, while arthropods were part of the diet only in the middle of the wet season between January and April.

Discussion

Reproduction

It has been shown throughout Africa that reproduction in *Mastomys natalensis* is associated with rainfall (Coetzee 1965; Taylor and Green 1976; Neal 1977; Swanepoel 1980; Chidumayo 1984; Bronner et al. 1988; Leirs et al. 1989; Perrin et al. 1992; Wirminghaus and Perrin 1993). Bronner et al. 1988 reported a correlation between rainfall two months previously and reproductive activity in female (but not male) *M. natalensis* from South Africa. A similar correlation was reported by Leirs and Verheyen (1995). The latter study, conducted over several years, included interannual variation in rainfall which, thus, strengthened the observed correlation. In the present study, reproductive activity of

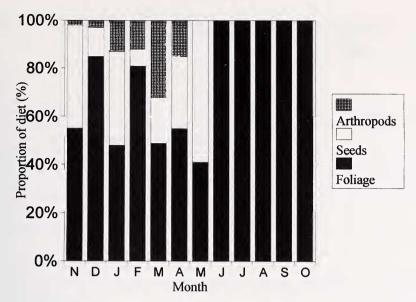


Fig. 4. Seasonal changes in (%) diet composition of *Mastomys natalensis* between November 1996 and October 1997 at eKundizeni Farm, Swaziland.

both male and female *M. natalensis* was correlated with rainfall in the previous month, although the strongest correlation in females was with rainfall two months previously. This supports the suggestion that rainfall is the ultimate factor in the timing of reproduction in female *M. natalensis* (Bronner et al. 1988). In males, in contrast, the strongest correlation was with rainfall in the same month. The reason for this is probably related to the fact that reproductive activity in females was defined by pregnancy, while in males it was defined by scrotal testes. Defined as such, males should be able to respond to rainfall quicker than females.

The litter size of *M. natalensis* reported here (11.4) is very similar to that reported from Morogoro in Tanzania (11.3; Leirs and Verheyen 1995) and that from Zambia (12.4; Chidumayo 1984). There were no differences in litter size between three different age classes of *M. natalensis* supporting the findings of Leirs and Verheyen (1995). Thus, there was no age-specific fecundity. Similar findings have also been reported for *Tatera leucogaster* (Perrin and Swanepoel 1987).

Age structure

The seasonal changes in age structure of *M. natalensis* described in this study are similar to those described in Tanzania (Leirs et al. 1993; Leirs and Verheyen 1995), and to those described by toothwear in South Africa (Coetzee 1965), Uganda (Neal 1977), and Zambia (Chidumayo 1984). *Mastomys natalensis* individuals seldom survive much beyond 12 months, and probably never breed in more than one season. Of the four mice, in this study, whose ages were estimated between 400 and 480 days, one of them was captured in July and probably would not have survived the dry season to breed in a second season. The other three mice were captured in the middle to late wet season and would, thus, have been immatures in the previous breeding season. The older age classes die off at the end of the breeding season (March/April) and are replaced by that season's offspring.

The monthly age structure of this population corresponded with the timing of reproductive activity of the mice and was dissimilar in the two breeding seasons. In the 1995/6

season, pregnant females were first captured in November and immature mice in December. In the 1996/7 season, pregnant females were first captured in December/January and immatures in February.

Diet

Mastomys natalensis exhibits gastro-intetinal and dental characteristics typical of an omnivorous murid rodent (Perrin and Curtis 1980). In this study M. natalensis appeared to be omnivorous, feeding on what food was available. In the dry season when seeds and arthropods are present in low numbers (LACK 1986), M. natalensis fed only on vegetative plant matter (probably leaves of grasses). In the wet when most grasses seed (VAN OUDT-SHOORN 1992) and arthropod numbers increase (LACK 1986), seeds and arthropods contributed up to 50% of the identifiable stomach contents. Similar observations have been made in Tanzania (Leirs et al. 1994; Leirs and Verheyen 1995). In the latter study, the diet of M. natalensis was predominantly vegetative plant matter, with arthropod consumption increasing in the wet seasons. Seeds were an important component of the diet during the long "masika" rains when reproduction was at its peak. In Uganda, Field (1975) reported that over 90% of the stomachs of M. natalensis contained insect remains which made up 20% of the diet by weight. In Kenya, based on faecal analysis of M. natalensis, grass seeds contributed the bulk of food eaten (OGUGE 1995). It is likely that seeds and vegetative plant matter are not digested to the same degree (Hansson 1970), and that therefore the results of faecal analysis are skewed toward food material that digests slowly. In Zimbabwe, seeds formed the main component of the diet of M. natalensis, while arthropods contributed significantly only in spring and summer (SWANEPOEL 1980). The latter study was conducted in an agricultural area, and it is thus likely that seeds would have been available throughout the year. In conclusion, it would appear that M. natalensis consumes seeds and arthropods when available, but survives on vegetative plant matter throughout the remainder of the year.

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Zusammenfassung

Fortpflanzungsbiologie, Altersstruktur und Nahrung von Mastomys natalensis (Muridae: Rodentia) im Grasland von Swaziland

In einem subtropischen Graslandgebiet in Swaziland wurden der zeitliche Verlauf der Fortpflanzung, monatliche Veränderungen in der Altersstruktur und die Nahrung von *Mastomys natalensis* untersucht. Die Vielzitzenratten wurden jeden Monat über einen Zeitraum von 25 Monaten gefangen. Das individuelle Alter der Tiere wurde mit Hilfe des Augenlinsengewichts geschätzt. Trächtige Weibchen und skrotale Männchen wurden nur in der Regenzeit festgestellt, wobei jahreszeitliche Differenzen im Beginn der Fortpflanzung mit dem Niederschlag korrelierten. Monatliche Veränderungen der Altersstruktur von *M. natalensis* wurden bestimmt durch das Auftauchen von Jungtieren in der Regenzeit und den Tod von fortpflanzungsaktiven Adulten in der folgenden Trockenzeit. Die Mägen von *M. natalensis* enthielten in der Trockenzeit vorwiegend vegetatives Pflanzenmaterial, in der Regenzeit bildeten Samen und Arthropoden einen wesentlichen Anteil.

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